Evolution of cooperation in public goods games with probabilistic participation (Theory of Biomathematics and its Applications IV)

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Abstract

Cooperation, defection, nonparticipation and withdrawal are well-known aspects of behavior in game-like activities in free societies. Hauert et al. showed that the voluntary Public Goods (PGG) game consisting of three pure strategies: cooperation, defection, and nonparticipation, can lead to the "rock-scissors-paper" cycle and maintain levels of cooperation. Here, we focus on the two-dimensional adaptive dynamics of cooperative investments and participation rates in the PGG, and consider the situation where individuals have two types of continuous-valued options: a probability of joining the game, and, if they do so, a level of cooperative investment.

1 Introduction

The reason for the emergence and maintenance of cooperative behavior is an enduring puzzle in biology and the social sciences. The nature of this puzzle is shown by social dilemmas, which may be characterized as follows [1]: groups of cooperators outperform groups of defectors, but defectors always outperform cooperators in any mixed group. This represents the classical conflict of interest between the individual and the community. Many theoretical and experimental investigations of cooperative behavior have employed the framework of the Public Goods game (PGG) [9], in other words, the multiperson Prisoner's Dilemma. Typical PGGs can be described as follows. Cooperators in an N-player group invest the same amount in a common pool and defectors do nothing at all. The total amount of investment is then multiplied by a factor r (> 1) and distributed equally among all members of the group despite the preceding different investment amounts. With $r < N$, each player is better off defecting than cooperating, irrespective of the other players' decisions, i.e., defection dominates cooperation. Cooperators are thus evolutionarily doomed by defectors. This is an example of a social dilemma, and equivalent to the well-known Prisoner's Dilemma in the case of $N = 2$.

Here we focus on the effects of voluntary participation on the evolution of cooperation. Voluntary participation appears to be the simplest mechanism that can be justified as an a priori option even under complete anonymity. The voluntary PGG that Hauert et al.[4][5] have defined consists of three pure strategies: cooperation, defection, and nonparticipation, in which players opt out of unpromising joint enterprises and instead rely on a small but fixed payoff. This system, in which the size of the group participating in the game varies stochastically, leads to a rotational dominating strategy among the three strategies that is comparable to the "rock-scissors-paper" cycle, and thus populations are prevented from ending up in mutual defection.

Instead of such discrete behavioral strategies, we intuitively consider individuals who are able to make continuously varying degrees of investment levels and also alter their participation rates

[10], It is natural that the degree of voluntary participation in profitable but risky joint enterprises is not assumed as all-or-nothing but rather as a continuous variable from the standpoint of diversification of risk, as well as from the viewpoint of co-operative investment. We thus extend the original voluntary PGG to co-evolutionary processes of two continuous traits.

1.1 The continuous voluntary PGG

In our model, each individual has a continuous strategy involving two traits, $(c, p) \in \mathbb{R}[0, 1]^2$. The first coordinate c represents the amount of investment that the individual makes in the PGG. The second, p, represents the probability of participation in this unpromising game. Here we consider a large well-mixed population of constant size M, whose members live on a small but fixed income σ. In this situation, N individuals are randomly selected and offered the option to participate in a PGG. Those who participate with probability p can contribute an investment at a cost c to themselves. All individual contributions are added up and multiplied with a constant factor r with $1 < r < N$. This amount is then shared equally among all participants. Each participant's payoff is given as a net benefit that consists of his or her share less the amount invested. A nonparticipant's payoff is a small but fixed σ independent of outcomes of the PGG, with $0 < \sigma < r - 1$ (it is better to be a nonparticipant than to be a defector without contributing at all, but better still to be in a group of cooperators making a full investment). If there is only one participants, we assume that this single player has to act as a nonparticipant and therefore the payoff is σ.

We will refer to the evolutionary game that results from our extension as the "continuous" voluntary PGG, and the original model defined by [4][5] as the "discrete" voluntary PGG, in order to distinguish between them. In the next section, we will attempt a mathematical analysis utilizing the adaptive dynamics theory for co-evolution of the two traits.

2 Adaptive dynamics

We use the mathematical framework of adaptive dynamics [2][7], to analyze the evolution resulting from a two-dimensional strategy (c, p). Consider a monomorphic resident in which every individual uses the same strategy, $\boldsymbol{x} = (c_x, p_x)$. Let us introduce the term *invasion fitness* $f_{\boldsymbol{x}}(\boldsymbol{y})$. It is the central concept of adaptive dynamics and denotes the growth rate of a rare mutant strategy $\boldsymbol{y} = (c_y, p_y)$ in the environment set by the monomorphic resident. We assume that the growth rate of a rare mutant $\boldsymbol{y}$ in a monomorphic resident $\boldsymbol{x}$ is determined by the replicator dynamics [7]. The invasion fitness is thus denoted by

$$f_{\boldsymbol{x}}(\boldsymbol{y}) = P(\boldsymbol{y}, \boldsymbol{x}) - P(\boldsymbol{x}, \boldsymbol{x}), \tag{2.1}$$

where $P(\boldsymbol{y}, \boldsymbol{x})$ is the payoff of a strategy $\boldsymbol{y}$ interacting with other $N - 1$ homogeneous strategies $\boldsymbol{x}$, and $P(\boldsymbol{x}, \boldsymbol{x})$ is the payoff of a homogenous group for $\boldsymbol{x}$. From the definition of the continuous voluntary PGG, we denote the payoff function $P(\boldsymbol{y}, \boldsymbol{x})$ as follows:

$$P(\boldsymbol{y}, \boldsymbol{x}) = p_y g_{\boldsymbol{x}}(\boldsymbol{y}) + (1 - p_y)\sigma, \tag{2.2}$$

where $g_{\boldsymbol{x}}(\boldsymbol{y})$ denotes the rare mutant $\boldsymbol{y}$'s expected payoff when $\boldsymbol{y}$ participates in the PGG with probability p_y and σ denotes the fixed payoff when $\boldsymbol{y}$ does not do so with probability $1 - p_y$.

The following calculations for $f_{\boldsymbol{x}}(\boldsymbol{y})$ are straightforward, similar to arguments in [5]. We will estimate the probability that S of the N individuals ($= N-1$ residents sampled + the mutant $\boldsymbol{y}$) are willing to join the PGG. In the case $S = 1$ (no resident individual participates), the mutant obtains the payoff σ according to assumption. This happens with probability $(1 - p_x)^{N-1}$. Meanwhile, when $S-1$ individuals among the sampled $N-1$ residents join the PGG ($S > 1$), the payoff for the

mutant y is $r((S-1)c_x+c_y)/S-c_y$. This event happens with probability $\binom{N-1}{S-1}(1-p_x)^{N-S}p_x^{S-1}$. Hence, $g_x(y)$ is given by

$$\begin{aligned} g_x(y) &= \sigma(1-p_x)^{N-1}+\sum_{S=2}^{N}\binom{N-1}{S-1}(1-p_x)^{N-S}p_x^{S-1}\left[\frac{r((S-1)c_x+c_y)}{S}-c_y\right] \\ &= \sigma+((r-1)c_x-\sigma)(1-z^{N-1})-F(z_x)(c_y-c_x), \end{aligned} \tag{2.3}$$

where $z_x = 1-p_x$ and $F(z_x)$ is defined by

$$F(z_x) = 1+(r-1)z_x^{N-1}-\frac{r(1-z_x^N)}{N(1-z_x)}. \tag{2.4}$$

$F(z_x)$ has been defined for the discrete voluntary PGG; it refers to the advantage of defectors over cooperators, depending only on the frequency of nonparticipating behavior: $z_x = 1-p_x$. We note that the set of roots of $F(z_x)$ in $[0,1]$ is a singleton set consisting only of $z_x = 1$ for $r \leq 2$, and in addition there is a unique interior root for $r > 2$. Thus, we obtain

$$f_x(y) = -p_xF(z_x)(c_y-c_x)+((r-1)c_x-\sigma)(1-z_x^{N-1})(p_y-p_x)-F(z_x)(c_y-c_x)(p_y-p_x), \tag{2.5}$$

that represents the Taylor expansion around $\boldsymbol{x} = (c_x, p_x)$.

The adaptive dynamics of the strategy $\boldsymbol{x}$ is then governed by the selection gradient as below, with the exception of the vicinity of its equilibrium points.

$$\boldsymbol{D}(\boldsymbol{x}) = \begin{pmatrix} \frac{\partial f_x(y)}{\partial c_y} \\ \frac{\partial f_x(y)}{\partial p_y} \end{pmatrix}_{y=x} = \begin{pmatrix} -(1-z_x)F(z_x) \\ ((r-1)c_x-\sigma)(1-z_x^{N-1}) \end{pmatrix}, \tag{2.6}$$

so that $\dot{\boldsymbol{x}} = \boldsymbol{D}(\boldsymbol{x})$. An example is given in Figure 1. This vector points in the direction of the maximal increase of the mutant's advantage over the resident population, that is, the adaptive dynamics suggests the most favorable direction [7]. Note that, in general, $\dot{\boldsymbol{x}} = m\boldsymbol{C}\boldsymbol{D}(\boldsymbol{x})$, where the matrix $\boldsymbol{C}$ is the variance-covariance matrix of the difference vector between the mutant's strategy and that of its ancestor, and m depends on the equilibrium for the population size and the mutational process [2]. For simplicity, in this paper we assume both a constant population size and an appropriate distribution of mutations occurring independently and similarly for each trait so that one can set $m\boldsymbol{C} = 1$ (unit matrix).

Equilibrium points of the adaptive dynamics are called singular strategies, and they are given by solutions of $\boldsymbol{D}(\boldsymbol{x}) = 0$. If there is no such solution, the trait $\boldsymbol{x}$ is always under directional pressure from the selection gradient. From Eq. (2.6), singular strategies of the continuous voluntary PGG are given by $\{(\sigma/(r-1), 1-\hat{z}) =: \boldsymbol{Q}\} \cup \{p = 0\}$ where $\hat{z}$ is the unique interior root of $F(z_x)$ for $r > 2$. For $r \leq 2$ the singular strategies are given by $p = 0$ only. The point $\boldsymbol{Q}$ and the line $p = 0$ correspond to the interior equilibrium and the nonparticipant-homogeneous state of the discrete voluntary PGG, respectively.

When the singular point $\boldsymbol{Q}$ exists, we obtain the Jacobian matrix at $\boldsymbol{Q}$ as follows:

$$\left.\frac{\partial \boldsymbol{D}(\boldsymbol{x})}{\partial \boldsymbol{x}}\right|_{\boldsymbol{x}=\boldsymbol{Q}} = \begin{pmatrix} 0 & (1-\hat{z})F'(\hat{z}) \\ (r-1)(1-\hat{z}^{N-1}) & 0 \end{pmatrix}. \tag{2.7}$$

The off-diagonal components are of opposite sign because $F'(\hat{z}) < 0$ [5], and the diagonal elements are 0. This implies that $\boldsymbol{Q}$ is a center surrounded locally by closed obits [6] (see also Fig.1). Along the singular line $p = 0$, other components except for the lower-diagonal component are equal to 0 as follows:

$$\left.\frac{\partial \boldsymbol{D}(\boldsymbol{x})}{\partial \boldsymbol{x}}\right|_{\boldsymbol{x}=(c_x,0)} = \begin{pmatrix} 0 & 0 \\ 0 & (N-1)((r-1)c_x-\sigma) \end{pmatrix}. \tag{2.8}$$

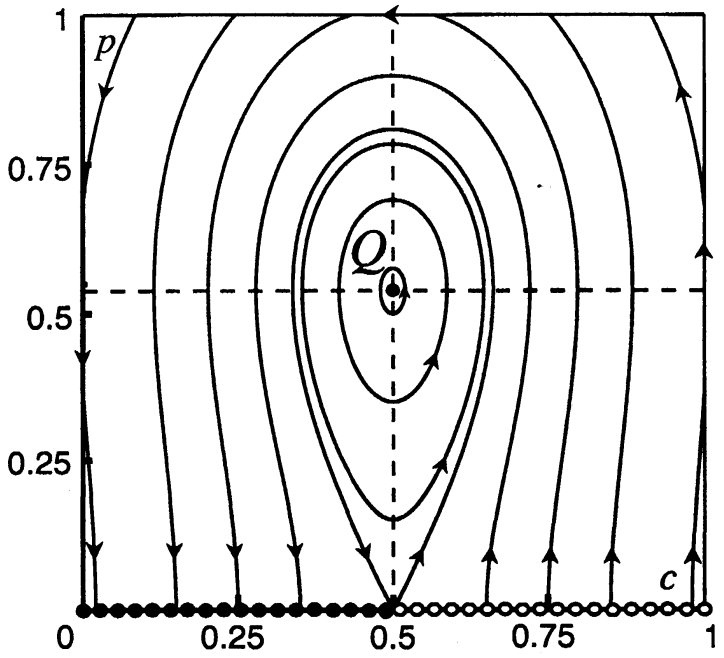

Figure 1: Selection gradient depicted by Eq. (2.6) for $N = 5, r = 3, \sigma = 1$. The horizontal axis is the investment level c. The vertical axis is the participation rate p. $\{\boldsymbol{Q}(0.5, 1-\hat{z})\} \cup \{p = 0\}$ is a set of singular strategies. $\hat{z} \approx 0.4613$. The two dashed lines $\{c = 0.5, p = 1-\hat{z}\}$ are the isoclines where the vertical and the horizontal selection pressure vanishes, respectively. The singular point $\boldsymbol{Q}$ is a center surrounded by closed orbits, i.e., neutrally stable. The critical point $(0.5, 0)$ divides the singular line $p = 0$ into the left segment of stable fixed points (closed circles) and the right segment of unstable fixed points (open circles).

The sign of the remaining element changes from positive to negative across a critical point $c_x = \sigma/(r-1)$ that divides the line into two segments consisting of stable fixed points (left side) and unstable fixed points (right side) .

3 Discussion

As illustrated in Fig.1, sufficiently far out orbits that start from the vicinity of $p = 0$ except for the critical point, are not closed and attracted to $p = 0$. Since the directional selection at investment level c is neutral on $p = 0$, what governs the evolution for the direction of $p = 0$ is neutral drift that breaks uniformity and causes a diversified population. In the case the induced evolutionary fate is unpredictable in line with the concept of the selection gradient based on a monomorphic population. Neutral drift plays a key role also in the evolutionary dynamics in the vicinity of $\boldsymbol{Q}$ where the selection pressure on both the directions of c and p is very weak (or vanishes at $\boldsymbol{Q}$). According to the adaptive dynamics theory considered, the population goes along closed orbits and cannot reach $\boldsymbol{Q}$ under the assumption that a resident population is monomorphic. However, if we relax the assumption and consider more realistic situation in which the mutation probability is not infinitely small, the directional selection pressure in the vicinity of $\boldsymbol{Q}$ is so weak that next mutations would occur before substitution of the resident strategy has been completed.

No satisfactory analysis of evolutionary diversification for the vicinity of the singular point, where directional selection pressure is no longer sufficient to select random mutants, has yet been published in the case of more than one dimension. Ito and Dieckmann [8] was the first to show

a natural process of evolutionary diversification in the two-dimensional case by considering co-evolution of two traits of the following types, one of which is subject to disruptive selection while the other is subject to weak directional selection.

Traditionally, the distinct existence of cooperators and defectors has been given a priori in theoretical discussions of social dilemmas. It is an essential theoretical challenge to justify such an assumption, because defectors outperform cooperators in any mixed group and cooperators should therefore be eliminated. Doebeli et al.[3] presented that, in the continuous Snowdrift game where there is relaxation of social dilemmas, large asymmetries in investment levels can arise from one-dimensional evolutionary branching. We will approach the issue of evolution of behavioral diversity in the two-dimensional case by using the continuous voluntary PGG proposed here in the near future.

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